

Melanic morph frequency in the peppered moth in the Manchester area

L. M. Cook^{1*}, R. L. H. Dennis¹ and G. S. Mani²

¹The Manchester Museum, University of Manchester, Manchester M13 9PL, UK

²Department of Physics, University of Manchester, Manchester M13 9PL, UK

Data are presented for the Manchester area, showing the recent change in frequency of the melanic morph *carbonaria* of the peppered moth *Biston betularia* (L.). The frequency has fallen from 90% in 1983 to below 10% at present; this decline shows that the phenomenon of industrial melanism, first noted in this species in Manchester, is now almost past.

Data from the Wirral peninsula, to the west of Manchester, published by C. A. Clarke and F. M. M. Clarke, show a slightly less rapid decline starting some ten years earlier from a lower maximum. Records from north-west Kent, published by B. K. West, also show a less intense decline from a lower peak several years in advance of the Manchester decline. The changes observed agree with a migration–selection model, which predicts subsidence of the plateau of high *carbonaria* frequency, with contraction from the edges. Selection in this model includes a non-visual fitness advantage of *carbonaria* homozygotes, a fitness difference associated with change in atmospheric sulphur dioxide concentration (which may act through differential crypsis) and frequency-dependent protection of rare forms. When all available data are compared, there is a negative relation between estimated fitness of *carbonaria* over the period of decline and initial level of atmospheric pollution.

Keywords: industrial melanism; peppered moth; *Biston*; natural selection

1. INTRODUCTION

Increase in frequency of melanic forms of the peppered moth *Biston betularia* was first recorded from the Manchester area, and inheritance of the forms and causes of spread were discussed, in the 19th and early 20th centuries (details in Kettlewell 1973; Majerus 1998). Whatever the precise causes, high frequencies of melanic morphs were clearly associated with urbanization and industrialization. Three categories of moth were distinguished: speckled black and white typicals, the uniform dominant black morph *carbonaria*, and an intermediate category *insularia*. This variation is due to several alleles producing different degrees of darkening. The moth is annual, and the rate of increase in melanic frequency in Manchester in the 19th century showed that *carbonaria* was then strongly advantageous. Kettlewell (1958, 1965, 1973) collected survey data for 1952–1970, when frequencies were quite static, showing the pattern in Britain, including the north-west region. Studies of a cline from extreme high to low frequencies of *carbonaria* from Liverpool to north Wales were made by Clarke & Sheppard (1963, 1966), Bishop (1972) and Whittle *et al.* (1976).

By the mid-1960s it was clear that the industrialized environment would change. Oil and electricity replaced coal as the main fuel, large cities underwent massive redevelopment and the old heavy industries declined. Smoke-control legislation consolidated a change already

in progress. There was rapid reduction in atmospheric smoke pollution in built-up areas and slower but nevertheless marked reduction in atmospheric sulphur dioxide. The geographic pattern of high and low SO₂ concentrations has always been more spread-out and less tied to urbanization than that of smoke, because the gas is more mobile and because some is produced by single large sources, such as power stations, which are good dispersers and not always in urban areas. Kettlewell's data show a plateau of high *carbonaria* frequency in urban and industrial regions with a low frequency to the west and south-west; this pattern fits better with the distribution of known SO₂ concentrations than with smoke levels (Lees *et al.* 1973; Bishop *et al.* 1975; Steward 1977).

A further survey was made in north-west England and north Wales to record the beginning of the anticipated change in morph frequency, and to investigate relative fitness (Cook *et al.* 1970; Askew *et al.* 1971; Bishop *et al.* 1978*a,b*). The area covered was from east of Manchester through the south Lancashire–north Cheshire mix of industrial towns and farmland, to Liverpool, and sites sampled by Clarke & Sheppard from there to north Wales. From Manchester to the Wirral the frequency of *carbonaria* was 90–98%. West of the river Dee and its estuary the frequency then dropped to 5% over a distance of 20–30 km. The frequency of *insularia* forms was and has remained low throughout, so that the visual appearance of a sample is determined by the ratio of *carbonaria* to typical. This is to be expected if the fitness difference between both *insularia* and typical and *insularia* and *carbonaria* is substantial. Under those circumstances

*Author for correspondence (lcook@fsl.scg.man.ac.uk).

Table 1. *Data on B. betularia frequencies from north-west England*

(GR: national grid reference 100 km and 10 km square of the sample; Caldý is in SJ 28. s.e.: binomial standard error of sample. Data for 1978 collected by J. A. Bishop, SJ 79 and SJ 89 by M. Dockery, SJ 78 by K. R. C. Neal and SJ 98 and SK 08 by S. H. Hind and Lyme Natural History Recording Group.)

location	GR	date	typical	<i>insularia</i>	<i>carbonaria</i>	total	<i>carbonaria</i> frequency (%)	s.e.
Meols	SJ 28	1978	12	2	45	59	76.3	5.5
Eastham	SJ 38	1978	12	3	106	121	87.6	3.0
Thingwall	SJ 28	1978	6	0	37	43	86.0	5.3
Urmston	SJ 79	1998	5	1	1	7	14.3	13.2
Hale	SJ 78	90–4	9	3	6	18	33.3	11.1
		95–8	8	0	1	9	11.1	10.5
Whalley Ra.	SJ 89	1993	3	0	2	5	40.0	21.9
Wilmslow	SJ 88	1996	42	4	11	57	19.3	5.2
		1997	43	4	5	52	9.6	4.1
		1998	24	0	1	25	4.0	3.9
Poynton	SJ 98	83–6	14	0	38	52	73.1	6.1
		87–9	8	0	34	42	81.0	6.1
		90–2	8	0	12	20	60.0	11.0
		93–5	22	0	7	29	24.1	7.9
		96–7	35	2	11	48	22.9	6.1
New Mills	SK 08	87–9	4	0	14	18	77.7	9.8
		91–6	6	0	3	9	33.3	15.7
N. Staffs	SK 06	96–7	9	1	1	11	9.1	8.7

insularia individuals always compete against a more successful morph and never reach a high frequency.

A few years later, overall change in England and Wales was tracked by using values from a survey made in 1983–84 (Cook *et al.* 1986). Individual samples were small, but they were widespread and allowed a morph frequency surface to be obtained by interpolation. This was compared with similar surfaces derived from Kettlewell's data sets for 1952–56 and 1957–70. The later set still included a plateau of *carbonaria* frequency of around 90% in the industrialized part of the country, but the area of the plateau had contracted, the cline separating low frequencies of south-west England and rural Wales having moved in a north-easterly direction. There is slow response when frequencies are very high or low, even under strong selection, the greatest change occurring at intermediate frequency. A shift to the north-east is therefore to be expected (Cook *et al.* 1990). Comparing the frequency surfaces for the different periods, we found that the fitness of *carbonaria* was 99% of that of typical for the transition from 1952 to 1970, confirming that the pattern was then effectively stable, whereas the change from the Kettlewell data to 1983–84 indicated an average relative fitness of 88% for *carbonaria* (Cook *et al.* 1986).

There was now a net disadvantage to the melanic form. Mani & Majerus (1993) give six localities in which a progressive decrease in melanic frequency has been recorded, and Grant *et al.* (1998) provide 12 further localities where there has been a drop between the Kettlewell surveys and the present. The most complete record is that of Sir Cyril and Lady Clarke (Clarke *et al.* 1990, 1994; Grant *et al.* 1996). Their site at Caldý, on the Wirral peninsula, was on the edge of the cline in 1959. Since then it has seen a drop from 93% to less than 10% *carbonaria*. We have assembled data for the Manchester area to

try to establish when and by how much the decline has occurred there.

2. DATA AND METHODS

Samples from moth trapping made between 1978 and 1998 are shown in table 1. The first three were collected on the Wirral peninsula in 1978 by J. A. Bishop. The figure obtained by the Clarkes for that year was 83.4%; these additional sites nearby provide further detail for the area. The others come from south of Manchester, where the frequency was around 96% in the early 1970s. Some (Hale, Poynton, New Mills) have been grouped into 10 km squares and/or for periods of a few years. Three records for successive years come from Wilmslow, about 15 km from Manchester city centre.

The *carbonaria* frequency was a few per cent in 1848. This form was prevalent by the 1870s, and had almost replaced the other forms by 1898, remaining at that level until the middle of the 20th century (Kettlewell (1973) gives references). Estimates for 1952 to the present are shown in figure 1. Those to 1974 are given by Bishop *et al.* (1978a), that for 1983–84 is from the frequency surface in Cook *et al.* (1986), and the rest are from table 1. At Caldý the starting frequency was slightly lower and the decline began at least a decade before that in Manchester (illustrated in Grant *et al.* (1996)). The subsequent rate of change was lower, so that by the late 1990s the frequencies in the two places are similar.

Decline has also occurred in other parts of the country (Mani & Majerus 1993; Grant *et al.* 1998). The pattern in north-west Kent is illustrated in figure 2, based on the data of West (1993, 1994). At the turn of the century *carbonaria* had not been observed there, but by the 1952–70 surveys it had risen to 65–89% in the north of the county (Kettlewell 1973). Evidently, it too achieved a lower peak and has declined at a lower rate than at Manchester.

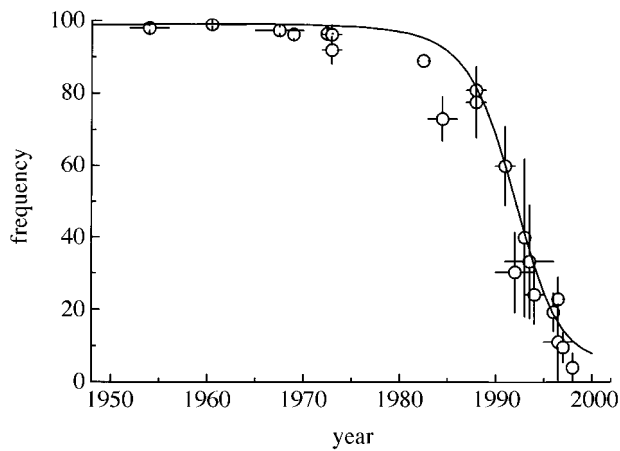


Figure 1. Change in frequency of the *carbonaria* form of the peppered moth *Biston betularia* (L.) in the Manchester area since 1950. Data are from Bishop *et al.* (1978a), Cook *et al.* (1986) and table 1. Vertical lines show standard error, horizontal lines range of years included. The curve is the theoretical prediction from the model of Mani (1982, 1990) with modified fitness.

Mani & Majerus (1993) compared data from six sites in different parts of the country, including Caldy, with the model of Mani (1982, 1990) and Clarke *et al.* (1985).

The model includes (i) substantial migration (Bishop 1972; Brakefield & Liebert 1990), (ii) a non-visual advantage to *carbonaria* homozygotes (Creed *et al.* 1980), (iii) fitness of *carbonaria* linked in some way to SO₂ concentration, and (iv) frequency-dependent protection of rare forms at extreme frequencies. The fitness component linked to SO₂ follows the pattern of change in atmospheric SO₂ concentration monitored in the vicinity of Caldy (Clarke *et al.* 1985). No disadvantage to *carbonaria* is assumed at the initial high concentration, followed by a linear drop in fitness for nearly two decades until a new level is reached where *carbonaria* has a fitness 85% of that of typical forms owing to this component. A description of how the model developed, and justification for these assumptions, is given elsewhere (Mani 1990). Data from the Wirral-north Wales area were used to decide on parameter values, so that the fit at Caldy was naturally very close. The chosen parameters then produced good predictions of the changes observed in other regions (Mani & Majerus 1993). The model was again used to provide the curves in figures 1 and 2, except that for Manchester it was necessary to change the final value of fitness component (iii), represented here as SO₂ concentration, from 85% to 55%. The selective effect appears to be more severe at Manchester than at Caldy.

3. DISCUSSION

Haldane (1924) pointed out that, to achieve the 19th century change, *carbonaria* must have had an advantage over typical of 50% per generation. This may be largely because of greater protection of melanic adults from predation as the environment became uniformly dark (Kettlewell 1973; Majerus 1998). If such selection was completely responsible for the change the population would have been entirely melanic by the 20th century. That did not occur, one possible reason, suggested by Haldane (1958), being that there was heterozygote advan-

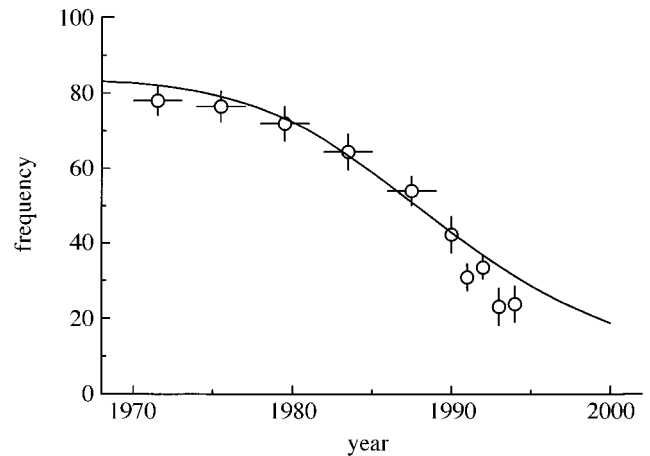


Figure 2. Change in frequency of *carbonaria* form in north-west Kent in records published by B. K. West. The curve is the theoretical prediction from the model of Mani (1982, 1990). Other details as for figure 1.

tage. When data from breeding experiments were examined by Creed *et al.* (1980), however, there appeared instead to be a non-visual advantage to *carbonaria* homozygotes while heterozygotes and typicals showed equal fitness. The insects are known to be highly mobile (Bishop 1972; Brakefield & Liebert 1990), and the steady level of about 95% probably indicates migration of typical forms from less industrialized regions (Bishop *et al.* 1978a; Cook & Mani 1980; Mani 1980, 1982).

The recent declines also indicate strong selection, this time against the melanics. If the simplest model is assumed, with constant selection and no migration, the Caldy data estimate the fitness of *carbonaria* as 85% of that of typicals, the Manchester data from 1954 as 79%, and the Kent data as 89%. These figures give us a rough picture of the selection. However, in all cases the constant selection curves lag below the data points in the middle of the sequence (see the graph of the Caldy data in Grant *et al.* (1996)). The more realistic modelling procedure removes this effect. When extracted, the SO₂-associated fitness is estimated as about 55% in Manchester compared with 85% for the other localities.

The results for Manchester and Kent and those of Mani & Majerus (1993) and Grant *et al.* (1998) allow 19 comparisons between early records with high frequencies of *carbonaria* and later records with low ones. Taken together, they suggest that selection against *carbonaria* may be greater in localities that initially were more heavily polluted (for regression of constant selection estimate on initial *carbonaria* frequency, $t=7.10$, $p<0.001$). SO₂ concentration was a good predictor of *carbonaria* frequency when the pattern was more or less stable (Steward 1977), and it is possible that the association indicates a direct effect on the polymorphism. Evidence from some other industrial melanic species seems to favour this interpretation (see, for example, Bishop & Cook 1980; Lees 1981). Alternatively or in addition, SO₂ may act by altering the composition of the flora on surfaces used as resting sites by the moths, so as to modify relative crypsis. It is well known that lichens and bryophytes are sensitive to acid rain deposition, and that they

disappeared from industrialized areas while unpolluted localities continued to have rich and diverse epiphyte floras (Creed *et al.* 1973; Ferry *et al.* 1973; Bates *et al.* 1996). Although the process is not a simple reversion, lichens have increased in extent and diversity where SO₂ concentration has fallen (Henderson-Sellers & Seaward 1979; Hawksworth & McManus 1989; Bates *et al.* 1990; Brakefield 1990). In the north-west, epiphyte patterns changed after the decline in atmospheric pollution (Bishop *et al.* 1975; Cook *et al.* 1990). A similar association of changes has occurred in The Netherlands (Brakefield 1990). Grant *et al.* (1996, 1998) question epiphyte change as a possible factor explaining the change in frequency, but if selective predation is involved, then anything likely to affect background colour or heterogeneity may be important.

One factor that has received attention is the location of resting moths during the day. Early experiments on matching of moths to background were carried out on tree trunks up to some 2 m from the ground (see Kettlewell 1973; Clarke & Sheppard 1966; Bishop *et al.* 1978*b*). In natural conditions adults usually settle much higher in trees, on small branches, and select their resting site with care (Mikkola 1979, 1984; Liebert & Brakefield 1987; Grant & Howlett 1988). These findings indicate that the relation of selection to type of background is complex. When the cline was well developed in the north-west region, however, the difference between rural areas to the west and urban ones to the east was immense. Within each habitat there was a strong correlation between the appearance of different parts of trees, different species of tree, and indeed between trees and other possible resting sites such as walls and bushes. It seems probable that the cline was set up, was maintained and has now decayed as a result of these gross differences in selection, modulated by migration. As Mani (1990) noted, 'The decline in the melanic frequencies in response to falling levels of air pollution presents an excellent opportunity for an intensive study both in the laboratory and in the field of gene action and non-visual selection effects. It would be a pity for the understanding of evolutionary ecology if we missed it.' The opportunity has now nearly gone.

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